# SIMULATI()X MODELING OF AMERICAN MARTEN (MARTES AMERICANA) P()PULATIONS: VULNERABILITY TO EXTINCTION 

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#### Abstract

 mumties across northern North Smerica. Martens are susceptible to local extinction from habitat alterations, trapping, and other factors. We R(:L) developed a population model called VORTEX to estimate extinction probabilities for maten poputations as a management tond. The modet permits managers to simulate various levels of timber harvesting, eonmereial trapping, and other lactors to estimate their effects on marten populations. This paper describes this model and illustrates its benclits by using marten data from the Creater lellowstone Ecosystem of northwestern $W$ yoming. Results are preliminary: Populations of 50 and 100 martens were simulated. The most optimistie secenario with populations of 100 ) individhats, no trapping, no logeing, and no migrants showed a probability ( $66^{\circ} \%$ ) of surviving 100 years. Extinction probabilities were sensitive to immigration and emigration rates. Numerons scenarios were simulated and howed a range of results. Results of population viability analysis can be tramslated into area requirements if densities are known or can be estimated. In turn, various habitat patehes and interconnecting eorridors can be examined for their ability to support viable marten populations. Population modeling is invahable to "adaptive management" of martens as well as other upecies


Key words: ulaptire management, Ameriean marten, demographic stochastieity, encirommental cariation, genetic sariation, extinctiom. Greater lellonestone Ecoststem, Population Viahility Analysis, simulation modeling, wilellife conscreatiom. \antes annericama.

American marten populations are susceptible to local extinction from labitat alterations, trapping, and other factors. For this reason and becalnse martens are sometimes considered an "indicator species" meder the National Forest Mamagement Act of 1976 by the U.S. Forest Service, it is important to have a means of estimating extinction probabilities for marten populations as a management tool. We developed such a means, a computer simulation model called VORTEX, that allows managers to carry out a population vulnerability assessment (Lacy 19993). This simulation permits managers to vary levels of timber harresting, eommereial trapping, and other factors and estimate their effeets on marten popwhations. Population management targets can bee explered with this procedure and, in the fiekd, marten populations matntained that ensure their persistence in the Fatee of foreseeahle extinction pressures (e.g., hab)itat fragmentation!. This paper deseribes this model and illustrates its utilit! in marten consemations and manatement.

Tha results presented in this paper are prelimanary Thes draw largely on marten popula-
tion data and ensirommental conditions in the Creater Yellowstone Ecosystem of northwestem Wyoming (Clark et al. 1989 [Demographic characteristics], Clark et al. 1989 [American marten]). The model can be rerm with better data from this area or data from other regions to estimate population vulnerability to local extinction under various conditions. This model has been used on a variety of rare and endangered species worldwide and has directlyaded their conservation and management (e.g., Lacy et al. 1989. Seal and Lacy 1989. Lacy and Clark 1990, Maguire et al. 1990, Seal and Lacy 1990, Lindemmayer et al. 1991, Lindemmaver et al. in press). We are confident it can aid American marten conservation and management too.

## E.tinction Process

To moderstand how VORTEX works, one must first understand the extinction process (see Shaffer 19s1. Gilpin and Soulé 1986, Clark et al. 1990 [Mamagement]). As populat tions beeonne fragmented and reduced in size, random lluctuations in population size can

[^0]become more important determinants of persistence than whether mean population growth is positive. Four classes of factors affect marten population survival: demographic, envirommental, catastrophic, and genetic variation. Fluctuations in population size can result from any or all of these fon kinds of stochastic (random) effects.

Demographic variation results from the probabilistic nature of birth and death proeesses: Even il the probability of an animal reproducing or dying is always constant, we expect that the actual proportion reproducing or dying within any time interval will vary aceording to a binomial distribution with mean equal to the probability of the event (p) and variance given by $\mathrm{V}=\mathrm{p} *(1-\mathrm{p}) / \mathrm{N}$ Demographic variation is thas intrinsie to the poputation and occurs because birth and death events are determined by random processes.

Enviromental variation (EV) is the variation in the probabilities of reproduction and mortality that ocem because of changes in the enviromment on an annual basis or other time scales. Thus, EV' impacts all individuals in the population simultaneously, changing the probabilities (means of the above binomial distributions) of birth and death. The sourees of EV are thus extrinsic to the population itself. due to weather, predator and prey populations, parasite loads, etc.

At the extreme of envirommental variation are events that could be temed catastrophes. Epidemic discases, severe storms, forest fires, or floods might kill a substantial portion of individuals in a population or disrupt a breeding season. Such events can impact a populattion more severely than conld be predicted from the normal range of envirommental variation in reproductive and mortality rates. Moreover, such catastrophes are often the proximate cause of the final extinction of local populations. Catastrophes are indivichally rare and umpredictahle, but most populations observed over a number of decades are likels to suffer one or more events that wonld commonly be termed catastroplies.

The tramsmission of genes is also a ramdom process, and genetic variability is lost from small populations due to drift and inbreeding. Inbreeding can canse decline in lecoundity and survival, exacerbating demographic problems and leading populations more rapidly toward
extinction Mright 197T. Ralls and Ballon 1953, Ralls et al. 195s).

The combination of these randem forcesdemographice stochasticit?, (emironmental variation, catastrophes, and genetic driftdestabilize small populations and mutnalls exatererbate the effects of each lexel of stochasticity. For example. the ramdom loss of erenetic variation that oecours as populations becomme small due to low fecomedity and high mortality in turn causes firthere decreased fecomedits, greater mortality, and susceptibilit! to cmirommental variation and catastrophes. The feedlack amone the varions ferces destabilizing small populations has been termed the "extanction vortex" (cilpin and Soulé 195(6).

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Population valality analysis (PVA) is a relattively recent procedure for estimating the a ialbility of small populations of organisms 'Shaffer 1981). Clank et al. (1990 [Population valailityl: I) defined PVA as a "procedure that allows wildlife managers to simmlate, using computer models, extinction processes that act on small populations. and therefore to assers their honer term viabilits." In both real and simulated populations, a number of interactine demographice, envirommental, catastrophice and genetie processes determine the wherablilit? of a population to extinction. Life talle andlyses yield aserage long-term projections of population growth (or dectine) but do not reveal the fluctuations in population siたe that would result from stochastic processes. Computer models can simulate the four interateding types of extinction processers and the eflecects of hoth deterministic and stochastic forcen (all be explored. By using this procedure: me can also simulate the outerone of alternation management options, such ats maintaninge habitat or increasing it, reducing mortality, upplementing the population, or other manasement options. As a result. Pli giver manatero a powerfin tool to adid in determining the valnerability of populations and in setting manaqement tareets. PI is especially usefill for managing rate and endangered upecien Clank
 al. 1990) [Vamagement]. Clarh et al. 19990 Pop)ulation viabilit!].
pli also provides quamtitative predictions of population growth, demographic Ilnctua-
tions, whd decat of quenctic variation, based on explicitly stated absmmptions. Thas, PVA can provide both an applicit model of population dyamics and the testable predictions that are necessany to bring the projection and management of wildlife populations into the realm of falsifiable science. The outcome of management based on PV:I can provide a test of the whequate of our understanding of the population dyamics. by comparison of quantified predictions to population performance, while achieving the goals of the management plan. PVA has also been coupled with other amation cal approaches, such as risk assessment and decision amalysis, to better manage species populations (Magnire 1956, Maguire et al. 1990).

## Iortex: Conplater Progran For Momelidg: Popllateon Dinanies

The complex interactions among demographic and genetic factors as they can impact populations of American martens were examined loy computer simulation modeling, using the progran VORTEX. VORTEX is a powerful, but user-friendly; program for modeling vertebrate population behavior by way of Uonte Carlo simulation of demographic and genetic events in the history of the population (Late 1993). Some of the algorithms in VORTEX were taken from a simulation program. SPCPC, written in BASIC by James Crier of Vorth Dakota State University (Grier 1980a. 19.5(0), ( Srier and Barclay 1988).

Vor'TEX molels population processes as discrete. secquential exents, with probabilistic ontcomes. VORTEX simulaters birth and death processess and the tramsmission of genes throngh the generations by generating random mombers to determine whe ther each amimal lives or diess. whother each adult female prochuces litters of sise $0,1,2,3,4$, or 5 during cath year: and which of the two atleles at a esenetic lesens are tramsmitted from cach par(ant to cath offisprines. Vortality and reproduction prolahilitien are sex-speceifice Fecomdity is assmaned to be independenst of age latter in animal reachom repproductive age $)$. Nortalits rates are speatied for cach pre-reproductive age class ame ofth whoductive-age amimals. The mating systeme com bee speceified to be either monogamons or polvernems. In wither casce, the user call sperifit that onls a monset of
the adult male population is in the breeding pool the remainder being excluded perhaps by social factors). Those males in the breeding pool all have equal probability of siring offspring.

Each simulation is started with a specified number of males and females of each prereprodnctive age class, and a specified number of mates and females of breeding age. Each animal in the initial population is assigned two unique alleles at some hypothetical genetic locus, and the user specifies the severity of inbreeding depression (expressed in the model as an increase in jwenile mortality in inbred animals). The computer program simulates and tracks the fate of each population and then outputs summary statistics on the probability of population extinction over specified time intervals, the mean time to extinction of those simulated populations that went extinct, the mean size of populations not yet extinct, and the levels of genetic variation remaining in any extant populations.
a population carrying capacity is imposed by a prohabilistic tmoncation of each age clats if the population size after breeding exceeds the specified carrying capacity. The program allows the user to model trends in the carrying capacity as linear increases or decreases across a specified number of years.

VORTEX models envirommental variation simplistically by selecting at the begiming of each year the population age-specific birth rates, age-specific death rates, and carying capacity from distributions with means and standard deviations specified by the user: EV in birth and death rates is simulated by sampling binomial distributions, with the standard deriations speeifying the ammal fluctuations in probabilities of reproduction and mortality. EV in reproduction and EV in mortality can be specified to be acting independently or jointly (correlated in so far as is possible for discrete binomial distributions).

Unfortumately, rarely do we have sufficient ficld data to estimate the fluctuations in birth and death rates, and in carrying capacity, for a wild population. (The population would have to be monitored for long enough to separate. statistically; sampling error, demographic variation in the mumber of breeders and deaths, and ammal variation in the probabilities of these events.) Lacking any data on ammal variation, a user can try various valnes, or set
$E V=0$ to model the fate of the population in the absence of any enviromental variation.

VORTEX can model catastrophes, the extreme of environmental variation, as events that occur with some specilied prohahility and reduce survival and reproduction for one year. A catastrophe is determined to ocemo if a randomly generated number between 0 and 1 is less than the probability of ocemrence (i.e., a binomial process is simulated). If a catastrophe occurs, the probability of breeding is multiplied be a severity factor specified by the user. Similarly, the probability of surviving each age class is multiplied by a severity factor specified by the user:

VORTEX also allows the user to supplement or harvest the population for any mumber of years in each simulation. The numbers of immigrants and removals are specified by age and sex. These numbers of immigrants and removals are modeled as constants, not dependent on population size. VORTEX outputs the observed rate of population growth separately for the years of supplementation/ harest and for the years without such management, and allows for reporting of extinction probahilities and population sizes at whatever time interval is desired (e.g., summary statistics can be output at $\overline{5}$-year intervals in a 100 -year simulation).

VORTEX can track multiple sul-populations, with user-specified migration among the units. The migration rates are entered for each pair of sub-populations as the proportion of animals in a sub-population that migrates to another sub-population (equivalently; the probability that an animal in one migrates to the other) each year: Because of migration (and, possibly, supplementation), there is the potential for population recolonization after local extinction. VORTEX tracks the time to first extinction, the time to recolonization, and the time to re-extinction.

Overall, the computer program simulates many of the complex levels of stochasticity that can affect a population. Becaluse VORTEX is a detailed model of population dymamies, it is not practical to examine all possible factors and all interactions that may affect a population. It is therefore incumbent upon each user to specify those parameters that (ail) be estimated reasonably; to leave out of the model those that are believed not to lave a substantial impact on the popmlation of inter-
est, and to explore al ranere of possilale valuen for paranceters that are potentialls important but wery imprecisely known.

VORTEX is compiled for we on merocomputers rombing the MS-DOS \icronolt Corp. operating system. VORTEX and a mannal deseribing its use are arailable from the office of the Captive Breedine Spectialist
 12101 Jolme Cake Ridge Road, Ipple Valler. Nimesota 55124. Deseriptions of the program strieture and underlyine assumptions are given in Lacy (1993). Detailed descriptions of the algorithms used in VorTEX. as well as the source code (in the C prosramming language), are given in Lindemmater et al. (I991).

> Popelation Biohogi Pirmieti:ks FOR MIRTEMS

We modeled a tariety of scemarios of marten population behat ion Fige. I). For thene preliminary amalyses age of reproduction. mean birth and age-specilic death rates. degree of polygyny, and sex ratio were obtained from published studies. Ase of first reproduction (time at which females give birth to their first litters) was set at 2 years for females. following the report by Strickland ed al. (1952) that 50 e of yearling lemale (approximate are 16 montis) msatly beeome pregnant, giving hirth about $\rightarrow$ month later: Although males sexually mature as yearling also, we assmmed that males matly do not breed sncerssfully until a year later their lime ollspring bom when sires are abont 3 y yars of ag(e).

Litter sizes were assumed to be typically 3 (6i0 $)^{2} \%$ of adult females). but occasionally smallor $\left(25^{\circ} \%\right.$ of addult females producine litters of 2 . $10 \%$ producing litters of 1 and $55^{2}$ e not breceding in an arcrage year). The mean litter size produced bey the distribution used is 2.53 me:m fecondity of athult femates $=2.40$. comsidering also the sec that fail to breed. The sen ration at birth was assmend to be l: 1 Clanh (et al. 1957).

Breeding males have been reported to have home ranges large emough to concompan the tervitories of three females (larh of all. 1959 [American marten]), and we therefore assumed that the are rage successliully hreeding male mates with three fomales. (iven the differential mortality assmed to act on the


Fig. 1. Cenarios tested for population vulnerability. and results obtained from 1000 simulations of 100 years for each acenario \ode, with boxes indicate manaqement decisions: nodes with eircles indicate random variables determined By population and habitat structure See lext for descriptions of seenarios. $\mathrm{PE}=$ probability of extinction; $\mathrm{TE}=$ mean tune to extinction. $\backslash=$ mean mun ber of martens in nonextinct populations after 100 s ears: $H=$ mean percent of initial heteroct quits remair in g in cotant populations at 100 years: $R=$ number of populations undergoing temporary extincthon and recolonization during the 100-ycar simulation.
sexen see below and the delayed breeding hy malen the expeeted ratio of adult $>2$ years of aqu males to adult $>1$ sear of age temales is 1:1.7f obtained from life table analysis some delult males $3^{-c} c$ assumed th bee excluded from the breeding population. (o) that. "ith Poisson distribution of repprofluctis sucess, the mean successfully breedines mak is mld are 3.0 litters. The calculation to keternme the necessan? proportion of adult males an the breedines pool to yield the destuad lequee if polysams. given the aqe-sex stra. of of the propulation and a Poisson distribut montactive success. are done automat. at to the UPTEEX program.


ond-year mortality of males, and $10^{\circ} \mathrm{c}$ annual mortality of males older than 2 years and females older than 1 vear. We further assumed that martens senesce after their tenth year. Given the mortality schedule, very few about $0.25 r^{c}$ animals would live beyond 10 years of aqe, and the assumption of senescence in the model has very little impact on the results obtained.

Lacking any information on the impact of inbreeding on survival of martens, we modeled the effect of inbreeding depression by assuming that inbreeding would depress survival to the extent (3.14 lethal equivalents) reported by Ralls et al. 1955) as the median of 4) mammalian populations. This level of imbreeding depression reduces the survival of the progeny of full-sib matings by about $32 \%$.

The populations studied by Ralls et al. were all captive (in zoos or research lahs, provided with unlimited food, and protected from exposure to disease, predation, and inclement weather. The impact of inbreeding on wild populations may he greater if inbreeding reduces an animals ability to cope with stresses.

Environmental variation in the above demographic parameters was modeled bs assuming that the probability of breeding bs adult females taries across years according to a binomial distribution with mean $95^{-}{ }^{c}$ a as deseribed abover and standard deviation of 5 'c Environmental variation in mortality rates was modeled for each age-sex class by setting the binomial standard deviation at one-fourth the mean (i.e., $50^{c} \pm 12.5^{\circ}$ r first year mortalit. $25^{\circ} \mathrm{c} \pm 6.25^{\circ} \mathrm{c}$ second-year mortality of males, and $10^{C_{c}} \pm 2.5^{c_{c}}$ amnual mortality of adults.

Two types of catastrophes were modeled. each with a probability of occurrence of $1 \widetilde{c}^{c}$ cach year of the simulation. The first type of catastrophe (e.g. disease) was assumed to kill. on average. $30^{\circ} \mathrm{c}$ of the population but to have no effect on reproduction of the sumtivors. A second type of catastrophe e.q.. fire was assumed also to kill $30^{c}$ of the animals but then to reduce reproduction by $10^{c}$ d during that year:

Population size and migration between populations are likely to vary widely among populations, and we tested several possible values (populations of 50 or 100 . with exchange of 0 . 2 . or 20 martens per sear to determine the sensitivity of a population to these parameters. The simulated populations were started at the stable age distribution calculated from the mortality schedule.

Finally: some aspects of the population dynamics are under direct control of resource managers. We examined the impact of trapping modeled as a harest of $20^{\circ} \mathrm{C}$ ammally and logeing modeled as a loss of $1 r^{c}$ of habitat per sear over 50 years on population sability to help define acceptable levels of human disturbance.

## SIVILATIO\ RFbしlit

The marten population scenarion listed above were simulated and result were expressed in terms of probability of extinction

PL. mean tine foretinction TE mamber of amimals 1 remaining at the coud of the wanlation in thone simulated populations mot extinct mean percent of initial hete roangovit remaining $[1$ and number of recolonizations R out of $100(0)$, imulations Fire 1. Each porpalation was simulated for 100 years and was repeated 1000 times for each eet of paratacters. These remults are not sufficient to peecits precisely the valnerabilit! of marten perpulations to local extinction. Withont detailed data on a -ppecific population of interest. wach comdusions camot be ohtained with the VokTEX simulation proqram or bs ans other technique. The results do. howeerer. illuntrate how computer simulation can be wed to examine the wherability of marten populations under warous possible scenarios. The ecenarios examined might represent the range of plansible values of population parameters that are poorl! known. or various powible manasement options, or as illustrated below both.

Life table analy is using the Leelie matrix approach Leslie 1945 . carried out bo the VORTEX program in addition to stochastic modeling. yields a mean expected population growth rate of $29.2 c$ with the bavic birth and death parameters specified above. and 3 . 'ch $^{c}$ mean population growth under the seenarios with survival reduced by goce due to trappmas Athough mean population growth was initially positive in each scenario modeled amd Growth observed in simulated populationclosely matched the expected population grow th calculated from the life table atenetio and demographic fluctuation reaulted in hish probability of population cettinction in dll cases in which the population was isolated from other populations. In the abence of exchange of migrants. only the ment optimastic ccenario no trapping. no logedime carre ime (apacit! of 100 ) had a prothathilit! $66^{\circ} \mathrm{c}$ of our viving 100 year Fig. 1. line $\&$. Without immigration and emorration the senetic wriabilite was rapidl? croded mpopulations of 50
 reduction an viahilit! inbrechang deprosion and erentually population crabl to ctine tion Fige oh. The celchanze of just a patir of migrants per year was wifficient to present damaging losee of acone tre variation Fis 3ath. Fechange of 10 pans per year lie a a population open to recular interchanse prevented

F.48 2. I ates of 1000 simulated populations with respect to proportion of initial heterozyosity (a) and population size h) over lot) years. Population parameters modeled as described in text, with mo trapping, no logging of habitat, and no immigratoon or cmigratom, in habitats with carry ing capacity ( K ) of 50 or 100 .


Fig. 3. Fates of 1000 simulated populations with respect toproportion of initial luteronctonts a and prypulation und (b) over 100 years. Population parameters modeted as described in text. with non trappinge mo logume of hathat cama ing capacity of 50 , and 0,2 , or 20 migrants exchanged per year
virtually any loss of genetic variation. In a few of the 1000 simulated populations in each seenario incorporatine migration, the modeled populations went temporarily extinct due to random fluctuations in reproduction and mortality: but they were successfully recolonized by immigrants (Fig. I, last columin).

Trapping, removing 20$)_{\%}$ of each age class ammailly, accelerated the loss of qenetic variation and consequent extinction in closed pop)-
ulations but was sustaimable in popmations that received contimed input of \& \& ele tic tarlattion va immigration Piges Aa.h Loescime a reduction in. Sore of the halbitat and therefine a reduction of 50 or in the halsitat carrsine capacity over 30 of the 100 ? (car of the smmlation, similarly accelerated inlmeedine and atinction when there was no migration. but was also sustamable if genetic variation was continuall! restored via exchange with other


Fis. P. Fales of foro simulated populations witla respect to proportion of initial heterozagosity (a) and population size
 h trapping mongeng of habitat. carrying capacits of 50 , and 0, 2, or 20 migrants cachanged per year.
populations (Fig. 1, lowner hadf), Whan immigration was low into trapped and or logged populations. the elfects of inbreeding depressed the meam population sizes below the camving capacitios modeled but did not lead to steady crosion of population vabilit? see Figs. far, b, and compare lines of Fig. 1 with 2 migrants to adjacent lines with 20 micrials .

## Disctission

Population modeling is essential to "adaptive management" of martens and other species. Adaptive management uses aetual management practices as an experiment to learn from, and modify as needed (Holling 1975). PVA not only permits trends in maten populations under current management to be
identified and quantified, but also permits detemination of those factors that exert intluence on the tremds. Modeling popnlation behavior is an important advantage in the eonservation and management of populations. There are few: if ims: other techniques currently arailable to syinthesize the emmulative impacts of a complex of factors on a population (Lindenmayer et al. 1991). This is important becaluse many recent studies have shown that the dymanies of populations change in relation to their size and context. As a result, P'A is nseful in addressing key marten management questions. For example, (1) What is the relationship between population size and population stability? (2) At what population size do random events become important and which of these factors are most eritical!? (3) What population target will ensure marten population persistenee in the management mit? Thus, PVA can be used to model these and other questions and the likely consequences of various management options.

The outeomes of management actions, Which must be monitored to permit adaptive management, provide a test of the adequacy of the model and data used to guide the management and provide refined data for improving the accuracy of PVA that will be used to guide future management. As better data and better models become arailable, PVA modeling should be repeated and reesamined. Used in these ways, PVA can be a key tool in adaptive management and a powerfil method for improving and testing our mederstanding of population biology:

It is important to recognize that, like ams model of the natural world, the results of PVA are only ats atecurate as the data that are fed into the model. Moreover, while PVI allows exploration of the interacting effeets of man! population processes, any PVA model is still ia simplified piecture of the real world. Factors that are not modeled or not eritically exanined might be influencing popmlation dyamies in mbnown ways (Lindemmayer et al. in press). Critical management plans shomld therefore ineorporate margins of error appropriate to the uncertainty abont the completeness of the models used, the accuracy of the data, and the potential eost of failed mamagement.

PVA is useful in identifyine declining maten population trends at an carly stage.
the essence of addaptive manarement thas allow ing pophations to be managed appropriatels before they beconne highly whemalle (e) extinction. PVI (am hodp identify pepmlatom processes that are likely to endaneer a population in the future if comective manasument atetions be.e. development of corviders tor allow erenetic and demoeraphice evehomed are not taken. Manaerement of a spereien is relatixcly inexpensise and organizationally simple when multiple healthy pepulations still evist compared to when the epecese hecomes endangered Clark et al. 1949 (D) ©igning and manalqing]).

Results of the marten PVI can lee tramslated into area requirements needed by local populations. ion ilhustration, assume that at manager wants to matintain a marten population, and beeanse of eircumstances berond his comtrol, with no possibility of immisration. The prediminary P\A results in Figures 1 and 2 indicate that well over 100 individuals ate needed. If a male and three female marten occupy about $3 \mathrm{~km}^{2}, 100$ martens would recquire $-5 \mathrm{~km}^{2}$. PVA results. combined with field studies of home ranges, can be used to determine habitat area needed for wild maten populations. \arious combinations of habitat patches and interconnecting corridors can be examined, in part, through PVis to explore extinction probabilities and manaerment options. Additionally, manarement options (am be further explored loy compline PVA with decision analysis Magnione of al. 1990). PVi combined with decision analus. using reliable fiedd data on marten populattions. offers the best adaptive manarement approach currently for this fascinatione forest (amivore.

## Latrothlaf (imid)


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Receited 26 June 1992
Aecepted 22 Fobruary 1993


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